

DRYOPTERIS GOLDIANA × INTERMEDIA — A
NATURAL WOODFERN CROSS OF NOTEWORTHY
MORPHOLOGY

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During the past ten years our studies of the species and hybrids of the woodferns, *Dryopteris*, of the United States have been gaining momentum. The pioneering field and herbarium researches of R. C. Benedict (1909) and E. T. Wherry (1961) over several decades have recently been supplemented by numerous cytogenetic investigations, especially those of Stanley Walker of the University of Liverpool (1962a, 1962b, and bibliography). Nevertheless, there are still vexing problems. For example, the relationships of the members of the *D. spinulosa* group are still in dispute (cf. Wagner and Hagenah, 1961). The confusing situation involving *D. clintoniana*, *D. wherryi*, and *D. celsa* in the area of New Jersey to North Carolina is still to be untangled (cf. Walker, op. cit.).

As is well known, hybridization is of major significance in creating the variation pattern of North American woodferns. However, a number of the interspecific crosses have yet to be described in sufficient detail to enable workers to recognize them readily. Some of the sterile hybrids found growing naturally are actually frequent to common members of the flora (e.g., *D. cristata* × *intermedia* and *D. intermedia* × *spinulosa*). Others are apparently extremely rare and sporadic, and it is one of the latter group with which we are concerned in this paper. The less common hybrid combinations are so poorly described in some cases that we find many herbarium collections which are misidentified and indeed many are not named in any way.

One of the most unusual of the rare hybrid woodferns is *Dryopteris goldiana* × *intermedia*, a cross which we might expect to occur freely in nature because of the more or less constant association of the parents. For some reason, however, the gametes of the parents must be incompatible to a

large extent. We have examined thousands of plants in dozens of localities without finding this cross. In fact, it was not until Evans discovered a specimen in August, 1963, growing with the parents in Vermont, that we were able to study living material of the cross at all. Charged with Evans' success in discovering material, we made an intensive search together in previously unexamined localities in Michigan, and succeeded in finding an additional plant with the same morphology. It seemed particularly desirable to collect additional material, because the first plant had the appearance of a "lop-sided" hybrid, the structure of the leaf apparently resembling *D. intermedia* much more than *D. goldiana*. Subsequently materials were borrowed from herbaria, and they were found also to conform to this pattern.

In the study of vascular plant hybrids we have come to expect primary crosses to be intermediate between the parents in most or all of their observable morphological details. This is especially true of fern hybrids, because practically all of them are what might be termed "F₁'s." Either they are sterile, or they are fertile and have become amphiploids presumably by direct transformation of "F₁'s." We were therefore greatly surprised to find that the cross of *D. goldiana* and *D. intermedia* resembled more a backcross to *D. intermedia* than a primary hybrid. Since the species characters of ferns are presumably controlled by a multitude of genetic factors, as a rule, they should, when combined, produce approximately intermediate conditions. Simple dominance or recessiveness should be the exception rather than the ordinary situation.

Accordingly, it is our purpose here to describe in some detail the cross *Dryopteris goldiana* × *intermedia* and to note briefly what we consider to be peculiarities of its morphology. We are indebted to the curators of the Gray Herbarium, the University of Pennsylvania, the Philadelphia Academy, the New England Botanical Club, and the New York Botanical Garden, for providing us their materials for examination. Also, we acknowledge R. C. Benedict and E. T. Wherry for their helpful letters; D. J. Hagenah for



Plate 1302. Whole fronds of *Dryopteris*. A. *D. intermedia*, Mich., Antrim Co., Evans 2027 (MICH). B. *D. goldiana* \times *intermedia*, same locality, Wagner 63144 (MICH). C. *D. goldiana* \times *intermedia*, Vermont, Windsor Co., Evans 1172 (MICH). D. *D. goldiana*, same locality as "A" and "B," Evans 2029 (MICH). (Scale = 10 cm.)

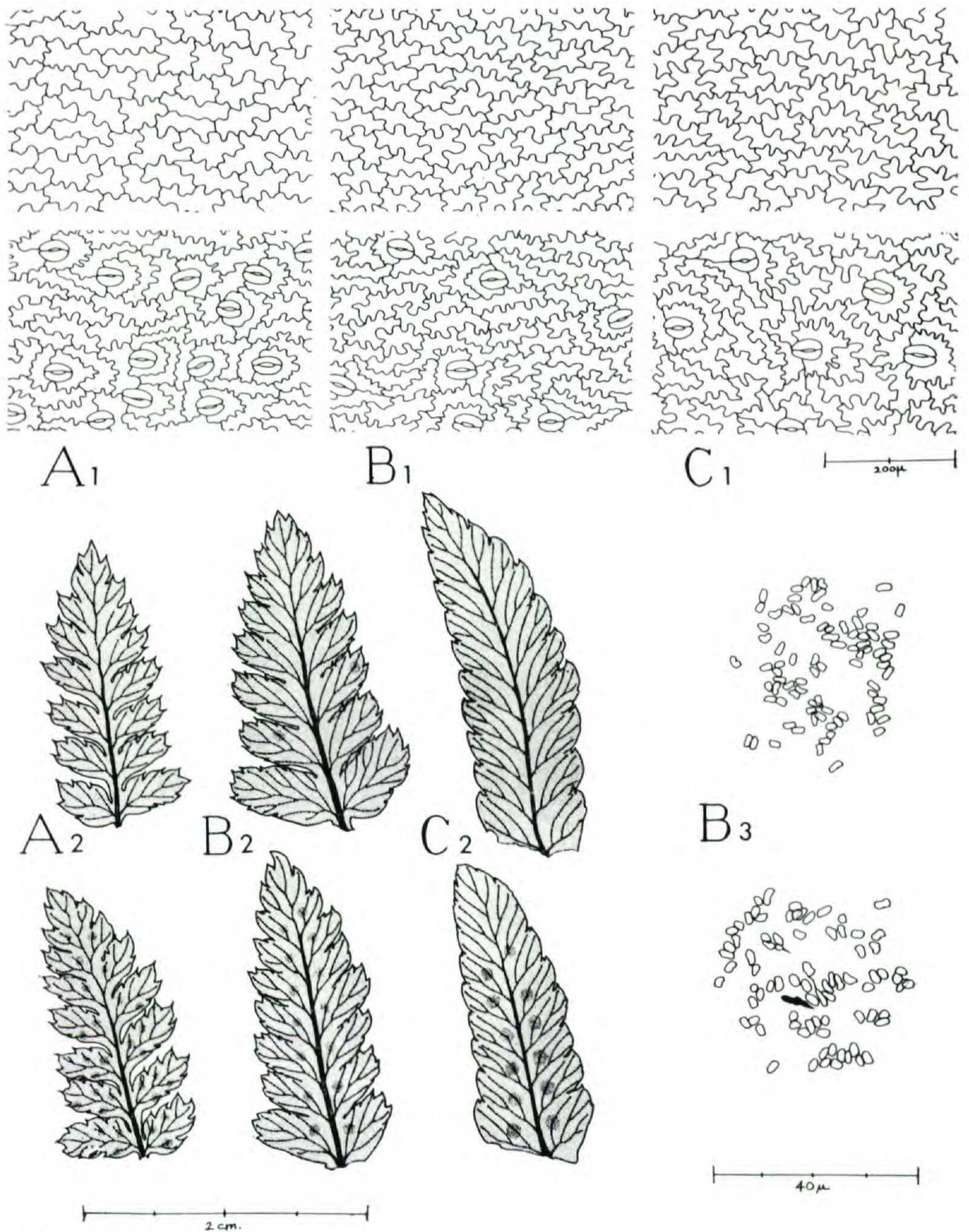


Figure 1. Anatomical and cytological details of *Dryopteris*. A. *D. intermedia*, Vermont, Wallingford, Evans on 7/18/1959. B. *D. goldiana* \times *intermedia*, Evans 1172. C. *D. goldiana*, Evans 1173-11 Subscript 1. Epidermal patterns, upper epidermis above, lower below. Subscript 2. Venation patterns of corresponding segments. Subscript 3. Chromosomes at meiotic metaphase of *D. goldiana* \times *intermedia*, Evans 1172, the upper figure showing no pairing, the lower showing a single pair, $2n = 82$.

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That collectors have often been in doubt as to what they had found is indicated by the question mark beside the hybrid formula on the New England Botanical Club specimen, and the fact that of the four sheets in the New York Botanical Garden, only one has an identification, a lightly pencilled "*D. goldiana* × *intermedia*" below the label at the bottom of the herbarium sheet. We wonder ourselves whether we have not overlooked this plant in the field because it resembles a very large individual of *D. intermedia* when examined casually (Plate 1302, B. C). Some of the specimens, especially those of Dutton and of Harlow cited below can be matched in cutting with almost perfect precision by selected specimens of the related *D. spinulosa*. In the very brief original description, Dowell (1908, basing his conclusions on the single Underwood collection) stated accurately that "In general appearance this fern looks like a large overgrown *D. intermedia* . . ."

Six collections from four states are now known of this scarce plant, and all of them conform closely to the same morphology. These collections may be cited as follows:

PENNSYLVANIA: Monroe Co., 5 mi. e. of La Anna, cut-over swamp, *R. C. Harlow* in 1946 (GH); Franklin Co., wooded rocky ravine, 5 mi. n. e. Ft. Loudon, *D. L. Emory* on May 26, 1963 (PENN). VERMONT: Rutland Co., Brandon, *D. L. Dutton* in 1923 (NEBC); Windsor Co., Barnard Gulf, steep, rocky, wooded slope, *A. M. Evans 1172* (MICH). NEW YORK: Chautauqua Co., Jamesville, *L. M. Underwood* in 1899 (4 sheets — NY). MICHIGAN: Antrim Co., T30N, R6W, Sect. 17, ca. 6 mi. n. of Mancelona, steep, springy hillside woods, *W. H. Wagner 63144* (MICH). A few collections which are patently *not* this hybrid are discussed below.

In Table 1 we have summarized some of the salient characters of the hybrid and the illustration (Plates 1302, 1303, and Figure 1) contain the most important information. It is therefore unnecessary to expand on these characters here, except to comment on the noteworthy, seemingly "unexpected," features. One of the details of the hybrid, namely its glandularity, does actually seem to show "dominance," al-

TABLE I

	<i>D. goldiana</i>	<i>D. gold.</i> × <i>int.</i>	<i>D. intermedia</i>
1. Habitat	Loamy, springy shaded slopes and swamp margins. Very local.	Loamy, springy shaded slopes and swamp margins. Sporadic.	Ubiquitous in various types of marshes, swamps, upland woods. Common to abundant.
2. Color of largest petiole scales	Shiny blackish chestnut except for narrow pale margins.	Shiny blackish chestnut in central area, but with broad pale margin.	Pale, except for more or less dark brownish area near attachment.
3. Pinna cutting	Lobed except at base.	1-pinnate except at base, the pinnules lobed.	2-pinnate.
4. Blade ratio, length/width	1.9 (1.7-2.2)	2.0 (1.8-2.2)	2.4 (2.3-2.6)
5. Petiolule length, center of rachis to costule departure	6.9 (5.5-8.0) mm.	5.0 (3.0-7.0) mm.	3.2 (2.0-4.0) mm.
6. Lamina (freshly dried)	Pale, dull green chartaceous.	Bright green chartaceous.	Bright shiny green, somewhat leathery.
7. Sori	In 1 row along each side of lobe.	1-several rows along each side of pinnule.	Several rows along each side of pinnule.
8. Indusia	Eglandular	Densely glandular	Densely glandular
9. Spores	Normal	Abortive	Normal
10. Chromosomes (Metaphase I)	41 pairs	82 singles (rarely 1 pair)	41 pairs

though from past experience we have come to expect this in all crosses involving *D. intermedia*. It is not necessarily a perfect picture (cf. Wagner and Hagenah, op. cit.), but in general the fact that the glandularity of *D. intermedia* is transferred completely to all of its hybrids makes this an

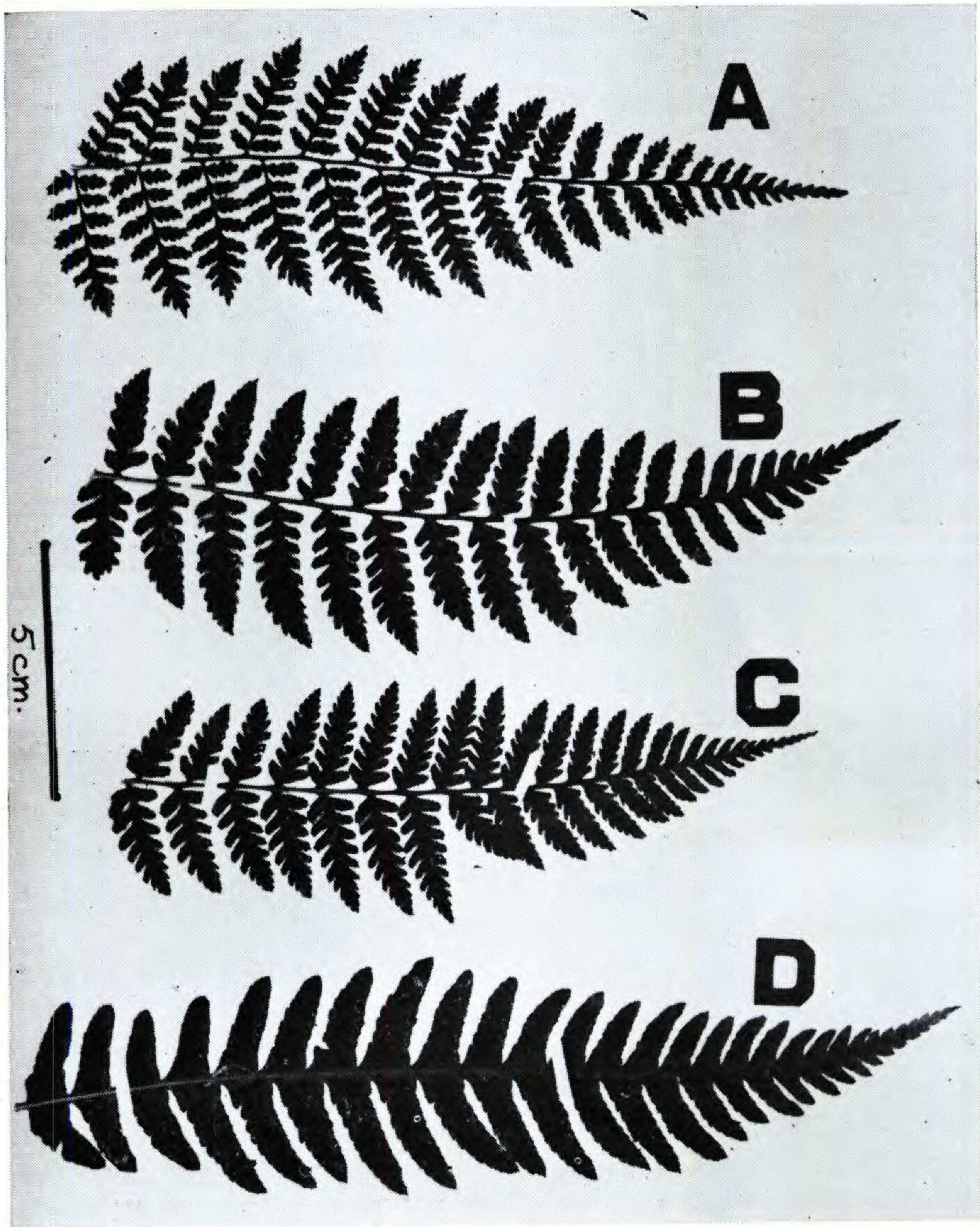


Plate 1303. Pinnae of *Dryopteris*. A. *D. intermedia*, Mich. Antrim Co., Evans 2031 (MICH). B. *D. goldiana* \times *intermedia*, same locality, Wagner 63144 (MICH). C. *D. goldiana* \times *intermedia*, Vermont, Windsor Co., Evans 1172 (MICH). D. *D. goldiana*, same locality as "A" and "B," Evans 2030 (MICH).

extremely valuable field character, as students of these plants are well aware. We cannot find that the indusia of *D. goldiana* \times *intermedia* are any less glandular than those of *D.*

intermedia. *D. goldiana* has entirely glabrous indusia. We conclude that in those hybrids we have examined, indusial glandularity is entirely dominant and the condition is not intermediate, the hybrid glands only scattered and sparse as we might postulate from the glabrousness of *D. goldiana*.

At present we have seen cytological figures only of the Vermont plant. There is nothing at all unexpected about the chromosome pairing behavior of the hybrid. Although in the related genus *Polystichum*, interspecific hybrids commonly show a considerable degree of pairing, in the genus *Dryopteris* unrelated genomes tend to lack pairing entirely or to show only casual pairs, as shown, in the present case, in Figure 1, [B₃]. This pairing condition is now well known in such other diploid hybrids as *D. dilatata* (Lake Superior "taxon") × *intermedia*, *D. dilatata* (L. Superior) × *marginalis*, and *D. intermedia* × *marginalis*.

The unexpected morphological feature of the hybrid involves the remarkably unbalanced appearance of the cutting of the leaf. Because the pinnæ are themselves entirely divided (cf. Plate 1303) instead of merely pinnatifid as in *D. goldiana*, the superficial appearance of the blade is greatly modified. Each segment with its own stalk tends to have an at least slightly twisted orientation (lost in drying in a press) and the surface and detailed outline of the blade thus appears "roughened." The result is that the frond presents a more lacy appearance than we would expect. The coarse, dull-green appearance of *D. goldiana* pinnæ seems vastly different from the more lacy, "spinulose" and shiny green appearance of *D. goldiana* × *intermedia*. Our analysis of this situation will be discussed below.

The following specimens exemplify collections which do not conform to our concept of *D. goldiana* × *intermedia*. They will be listed according to the names placed on the labels, and the reasons for our interpretations presented:

1. "Dryopteris celsa, *D. goldiana* × *spinulosa*?, *D. goldiana* × *intermedia*." MARYLAND: Harford Co., rocky woods on Mason's property, E. T. Wherry on 8/24/41 (PENN, PH). The two specimens do not agree with *D. goldiana* × *intermedia* in the following details: (a) the secondary segments are more broadly adnate and not so deeply incised;

(b) the texture is firmer, more leathery; and (c) the basal pinnae are more triangular. Comparison with our own materials of "*D. wherryi*" \times *intermedia* from Harford Co., Maryland, plus the various illustrations of *D. \times separabilis* (*D. celsa* \times *intermedia*) including those of Walker (1959) indicates that the specimens cited are closer to these than *D. goldiana* \times *intermedia*. (It should be mentioned here that there is a real possibility that "*D. wherryi*" = *D. celsa*, and that "*D. wherryi* \times *intermedia*" = *D. \times separabilis*. Current investigations are under way to analyze this situation.)

2. "*D. goldiana* \times *intermedia*." VERMONT: Bennington Co., Dorset, *E. H. Terry* on 11/6/1915 (NEBC). This specimen is almost surely some other woodfern hybrid combination. It is sterile (as judged from the sporangial contents), and the blade only is represented (the petiole is missing). Nevertheless, three characters do stand out: (a) the complete absence of glandularity; (b) the full or almost full adnation of the basis of the secondary segments; and (c) the triangular basal pinnae. The specimen is probably *D. clintoniana* \times *spinulosa*. (It is conceivable that it could represent *D. goldiana* \times *spinulosa*, which is another cross that has apparently never been clearly described, and with which we are as yet unfamiliar.)

3. "*D. goldiana* \times *intermedia*?" VERMONT: probably Rutland Co., Ex herb. *G. A. Woolson* (NY). According to the annotation, the specimen, which comprises only the upper part of the blade, has "some indusia glandular, but glands few, minute." Our search under the high-powered dissecting microscope, supplemented by indusial dissections treated in lactic acid, failed to expose any glands. We wonder, therefore, whether the earlier annotator did not see some whitish spores which have accumulated in the folds of the dried and curled indusia of this specimen. In any event, the cutting of the pinnae seems to be exactly that of *D. goldiana*. There is nothing about the blade structure that suggests influence of *D. intermedia*. Moreover, the spores of the fully developed sporangia are normal, as in *D. goldiana*.

The specimens of "*D. goldiana* \times *intermedia*" noted directly above differ from that hybrid, as we know it, and must be re-interpreted. Those specimens which we have cited earlier as representing true *D. goldiana* \times *intermedia* make a quite uniform and distinctive series, all showing the noteworthy morphological feature to be discussed below.

We have endeavored to analyze what it is that makes this hybrid appear to be so unequal an intermediate in gross aspect, being closer in the apparent structure of its fronds to one of its parents than the other. No one familiar with the species and hybrids of woodferns in eastern North America will fail to notice the close superficial similarity of

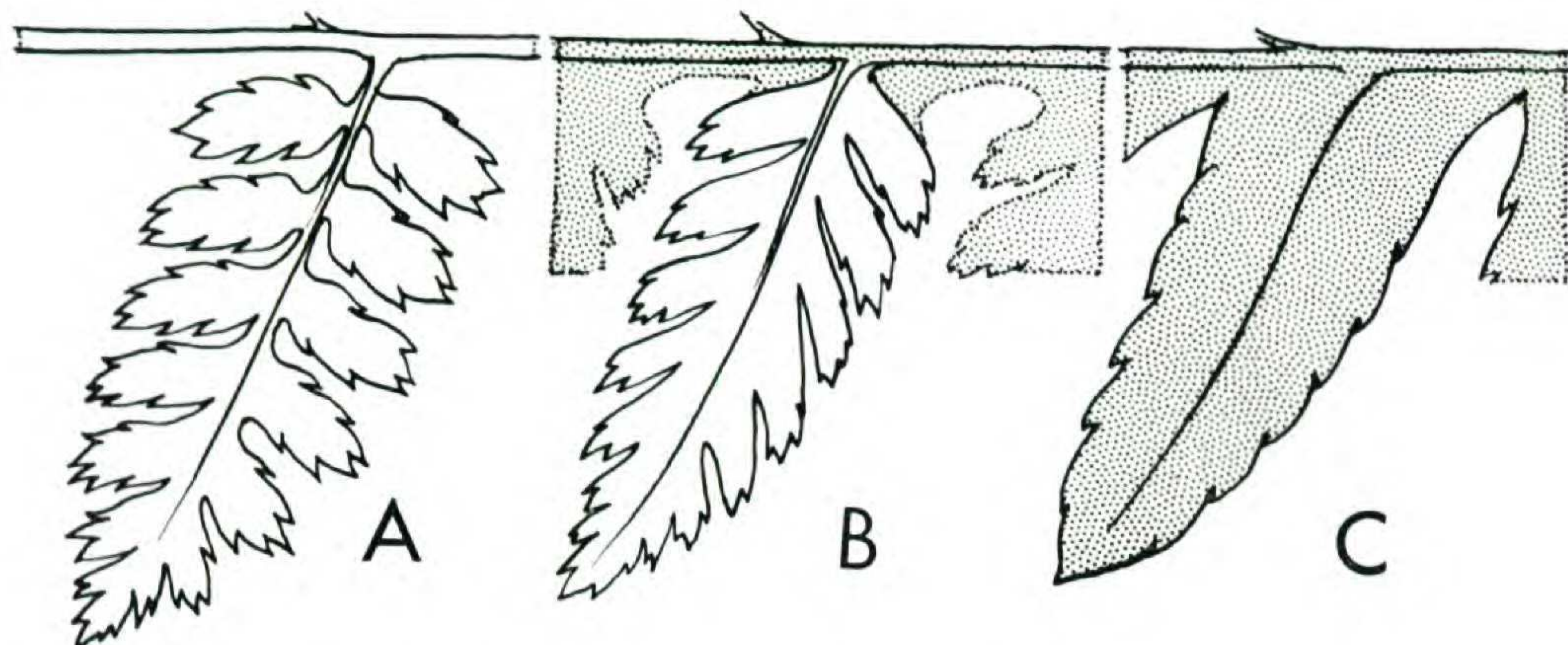


Figure 2. Hypothetical diagram showing corresponding leaf parts of A. *D. intermedia*, B. *D. goldiana* \times *intermedia*, and C. *D. goldiana*. The shaded area in "B" suggests what might seem to be a more intermediate "compromise" (i.e., the basal attachment more adnate and the costal wing more developed) between the segment bases of the parents than actually does exist in the cross.

the hybrid frond to *D. intermedia*. It is our conclusion that this seeming proximity to one of the parents can be ascribed to the cutting of the segments alone, for (as shown in the summation of characters in Table 1) the plant is actually a good intermediate in most other respects.

The attachments of the secondary divisions of the frond of the hybrid are not intermediate. In *D. goldiana* the secondary divisions are mere lobes, attached so broadly that they are actually confluent with the adjacent segments, as shown in Plate 1303 and Figure 2, C. There is a laminar wing, therefore, that runs along most of the pinnæ on either side of the costa. In *D. intermedia*, on the contrary, the secondary divisions are truly pinnules (themselves deeply pinnate), and the secondary divisions are of course attached by obvious, fully contracted stalks. There is no well developed laminar wing along the costa. One looking merely at the attachments of the secondary segments would expect in an intermediate hybrid that they would show a broad attachment, as shown in the hypothetical diagram (Fig. 2, B, the shaded area), but such is not the case. The fact is that the attachment of the pinnules is almost exactly as it is in *D. intermedia*.

This situation is a very good illustration of the possible dangers of quantifying taxonomic characters without reference to morphological knowledge. If we concentrated alone on the attachments of the secondary segments as a basis of comparison, we would conclude, as shown above, that *D. goldiana* is “fully adnate.” Therefore, quantitatively, we might say that “adnation = 1.” *D. intermedia* is not adnate at all; therefore its “adnation = 0.” The hybrid, if intermediate, should have the condition, “adnation = 0.5.” But it does not: quantitatively it shows the same as *D. intermedia* — “adnation = 0.”

But now, if we look over the whole frond structure, we find a different picture. The situation, in terms of frond division or leaflet formation, is in fact nicely intermediate. *D. goldiana* is 1-pinnate; *D. intermedia* is 3-pinnate; and their hybrid is 2-pinnate. From the standpoint of ontogeny, *D. goldiana* crosiers develop true leaflets (i. e., non-adnate, obviously stalked segments) only at the earliest stage, so that the subsequently formed segments are merely lobes at best. *D. intermedia* crosiers, on the other hand, continue their leaflet formation after the earliest stage. First they form the primary leaflets (the pinnæ), next they form the secondary leaflets (the pinnules), and finally they divide into tertiary leaflets (ultimate or tertiary pinnules). The hybrid is thus intermediate morphogenetically: the earliest stage is the same, the secondary stage is the same, but the tertiary stage is lacking — exactly what would be expected ontogenetically in a perfect intermediate.

What this means in terms of secondary-segment attachments is that they can be interpreted only in relation to the whole of the morphogenetic process that leads to leaflet formation. Thus the process of pinnation in this case transcends the details of the simple description of segment outlines of a given order (as shown in Figure 2). What this means in terms of superficial appearance to the field and herbarium botanist is that the frond of the hybrid seems to match *D. intermedia* much more closely than it does *D. goldiana*. The eye sees a myriad of individual segments,

each with its own stalk and orientation, so that the frond has approximately the same decomposed and highly complex aspect with which we are familiar in *D. intermedia*. The leaf of *D. goldiana* appears merely "streamlined" and simple because of its nearly flat, only deeply lobed pinnæ.

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LITERATURE CITED

- BENEDICT, R. C. 1909. New hybrids in *Dryopteris*. Bull. Torrey Club **36**: 41-49.
- DOWELL, PHILIP. 1908. New ferns described as hybrids in the genus *Dryopteris*. Bull. Torrey Club **35**: 135-140.
- SMALL, J. K. 1938. Ferns of the southeastern states. Lancaster, Pa.
- WAGNER, W. H. JR. AND DALE J. HAGENAH. 1962. *Dryopteris* in the Huron Mountain Club Area of Michigan. Brittonia **14**: 90-100.
- WALKER, STANLEY. 1959. Cytotaxonomic studies of some North American species of *Dryopteris*. Amer. Fern Jour. **49**: 104-112.
- , 1962a. Further studies in the genus *Dryopteris*: The origin of *D. clintoniana*, *D. celsa*, and related taxa. Amer. Jour. Bot. **49**: 497-503.
- , 1962b. The problem of *Dryopteris leedsii*. Amer. Jour. Bot. **49**: 971-974.
- WHERRY, E. T. 1961. The fern guide. Doubleday and Co. Garden City, New York.